Effects of Structural Complexity in Created Oyster Reefs on the Foraging Success of Red Drum (*Sciaenops ocellatus)* on Grass Shrimp (*Palaemonetes pugio*)

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Abstract

Oyster reefs created by *Crassostrea virginica* have been shown to be some of the most productive habitats in an estuarine ecosystem. There are many reasons behind this, but the one most focused on is how structurally complex oyster reefs affect predator-prey relationships on a trophic level. Treatments of varying complexity, with prey density scaled to the habitat complexity were used in a laboratory setting, using red drum (*Sciaenops ocellatus*) and daggerblade grass shrimp (*Palaemonetes pugio*) in order to test how differences in habitat complexity affect the foraging efficiency of the red drum. Results of these experiments show that the predation success of red drum on grass shrimp differed significantly only among reefs of different volume (density). Reef height and interstitial space did not influence foraging success. The results also show that a threshold level exists, showing that there is a point where added complexity fails to enhance refuge value. Oyster reef complexity, as measured by reef volume (density) significantly influences predation success; furthermore, there appears to be a threshold level at which further increasing complexity does not provide added benefits.

Introduction

The effects of predation on organizing biotic communities has been one of the most interesting studied areas in modern ecology (Savino and Stein 1982, Dill and Fraser 1984, Werner et al 1983). Predation is one of the most important governing patterns in natural systems (Sih et al 1998). It can broadly be defined as any interaction that leads to the flow of energy from one organism to another (Sih 1982). Predation can have multiple effects on the prey's behavior within a biotic community: habitat use, time of activity, diet, and foraging methods all can be affected by predation (Savino and Stein 1982, Dill and Fraser 1984, Werner et al 1983). Furthermore, in response to these behavioral changes, encounter rates between predator and prey may be altered as prey try to evade and seek sanctuary from predation (Savino and Stein 1989)

Near shore coastal aquatic communities are normally where predation is the most intense (Orth et al 1984, Clark et al 2003). It is also in these communities where physical structure can provide prey some relief from the most intense predation. Physical structure enhances the preys' ability to avoid predation by reducing encounter rates and foraging efficiency (Graboswki and Powers 2004). As such, enhanced structural complexity is often assumed to reduce prey vulnerability, hence decreasing predation success, and overall affecting community dynamics. Habitat structure can be defined as any abiotic or biotic physical structure in space, which supports plant and animal communities (Bell et al 1991). The ecological importance of more complex habitats is often generalized after the results were either increased availability of resources or improved refuge space associated with more intricate habitats are invoked as mechanisms. Habitat complexity can be grouped into two categories: quantitative and qualitative. Quantitative refers to the amount or density of structures, while qualitative refers to the heterogeneity or diversity of structures. Most experiments (Mattila et al 2008, Heck and Canion 2009, Gotceitas and Colgan 1989) have compensated for the quantitative category, in which all of the sea grass measurements were calculated as densities.

The relationship between habitat complexity (defined by quantitative measures of complexity) and predator efficiency has been described in different ways; although many studies agree that there is a non-linear relationship. Specifically, Nelson (1979) originally proposed a step function to describe the non-linear relationship between foraging efficiency and habitat complexity and numerous studies supported this general observation. Recently however, Mattilla et al (2008) and Canion and Heck (2009) proposed that increasing habitat complexity subsequently would increase predator and prey abundances in natural biotic communities. While other studies previously kept prey density constant among treatment levels, these two studies have increased prey densities with increasing habitat complexity to better mimic what happens in nature. In varying prey and predator densities to mimic natural densities, Mattila et al. (2008) found that increasing habitat complexity (shoot density) failed to increase prey survival rates. It is suggested that the benefits of increased habitat complexity may thus be negated by effects of increased densities. However, all of these studies have been completed in vegetated systems where the shoot density of the vegetation is varied as a measure of complexity; whether these results apply to other types of complex environments, and whether variation in the qualitative aspects of the structure have an impact are also important questions.

In coastal and estuarine environments along the coast of the southeastern United States, eastern oyster reefs (*Crassostrea virginica*) are an important part of the ecosystem. The reefs provide a significant amount of habitat structure to the local ecosystem. Healthy reefs provide a structural and ecologically complex habitat for many species on all trophic levels. The reefs have been called “ecosystem engineers” due to the many services they provide to the surrounding environment (Jones et al. 1994; Dame 1996; Lenihan 1999). Examples of services provided include: (1) benthic-pelagic coupling, (2) seston filtration, (3) provision of nesting habitat and creation of feeding habitat (Coen et al. 2007). Most importantly, the structure that the oyster reef creates is valuable as a protective habitat for many fish and crustaceans. Complex oyster reef habitats, in comparison to mud bottoms, generally have been found to support greater abundances of fish and invertebrates (Plunket and La Peyre 2005). However, within reef systems, it is unclear if the relationship of increasing complexity has a linear relationship with abundance of fish and invertebrates, and if refuge provision may be the mechanism that accounts for increased abundances. Furthermore, the difference between quantity of habitat (amount of oyster reef), and qualitative measures (i.e., interstitial space availability) has not been considered in considering the value of these reef structures for prey survival.

While there are many studies evaluating complexity and prey survival within seagrass systems (Mattila et al 2008, Heck and Canion 2009, Heck and Thoman 1981), few controlled laboratory studies have examined how fish, and, specifically, fish foraging success is impacted by oyster reef complexity. Even fewer studies have been done correlating how interstitial space may affect predator-prey interactions within oyster reef habitats. Humphries (2010) found that when a predator-prey combination (grass shrimp-redfish) was subjected to four different levels of reef complexity, there was a threshold of complexity above, which predation levels ceased to increase, supporting the non-linear model of complexity and prey survival model. However, during this study, prey density levels were kept constant among varying oyster reefs, and only quantitative complexity (i.e., shell density) was considered. The goal of this study was to explore the relationship between oyster reef structural complexity measures of both quantity (volume) and quality (interstitial space) and the foraging success of a common predator (redfish) on grass shrimp. Furthermore, following recommendations of Mattila et al. (2008), I varied prey density with habitat complexity. In a controlled laboratory experiment, we tested the effects of six levels of oyster reef complexities, four complexities involving only volume, and two complexities based on arrangement of space, on the foraging success of wild red drum (*Sciaenops occellatus*) on grass shrimp (*Palaemontes pugio*). We predicted that for each predator-prey combination, as reef complexity and interstitial space increases, the predation success will decrease.

Materials and Methods

Experimental Predator:

Red drum (redfish; *Sciaenops ocellatus*) is a common, estuarine dwelling species of fish found in the northern Gulf of Mexico. Redfish are very important to the commercial and recreational fishing industries along the Gulf Coast. They are large, solitary fish normally found in quiet waters of shallow bays. During the fall many redfish migrate to the northern Gulf of Mexico to spawn, then returning during the spring from the ocean. Red drum are opportunistic feeders throughout their whole life (Boothby and Avault 1971). They use mechanoreception as their primary foraging behavior and vision secondary (Liao and Chang 2003). Adult redfish feed on a variety of prey, including many shrimp species (*L. setiferus, P.pugio, and P. aztecus*) during portions of the year.

Experimental Prey

Grass shrimp (*Palaemonetes pugio*) are one of the most abundant species of caridean shrimp found in estuarine habitats (Leight et al 2005). They provide a valuable link in food webs. They are detrivores, playing an important role by recycling nutrients in a marsh ecosystem. Shrimp are also an important food source for many estuarine-dwelling fish species, including red drum. Their main predators include small, juvenile species of fish. *P. pugio* tend to be active during the night, which helps minimize their contact with visual predators. *P. pugio* are nearly transparent in appearance; they use this appearance, in combination with reduced motion, in order to become nearly invisible to predators. Grass shrimp also have quick, short popping reflexes that allow them to escape their predators' grasp. In the presence of predators, grass shrimp select oyster shell pyramids over seagrass and shallow water habitats (Eggleston et al 1999).

Collection and Maintenance of Predator and Prey

The 10 redfish used for this experiment were collected via hook and line behind the LUMCON facility in Cocodrie, Louisiana. They were transported using aquaculture tanks with airstones provided by Louisiana State University's Aquaculture Research Station. All redfish used in this experiment measured between 31-37 cm (33.0 ± 2.0 cm).

Grass shrimp collected in the experiment were collected with a bag seine (5 x 2 m bag seine composed of 3 mm square delta mesh) at two different locations in south Louisiana. One set of shrimp were collected in ponds at Cypremort Point State Park, St.Mary Parish, Louisiana and the other set were collected in the ponds in front of the LUMCON facility in Cocodrie, Louisiana. All shrimp used in this experiment measured between 19-43 mm (31.1 ± 6.5 mm). Weights of the shrimp ranged from 0.059-0.799 g, averaging (0.3245±0.1961 g). Gravid females were included.

All predator and prey species were held in recirculating tanks (350 liters) equipped with bio-filters (AST Bead Filter, Aquaculture Systems Technologies, LLC., New Orleans, Louisiana) prior to, and during the experiments._Redfish were fed bait live grass shrimp during captivity, while the shrimp were fed wet cat food.

Water quality (e.g., salinity, temperature, DO, ammonia) was monitored in the holding tanks. Overhead fluorescent lights (40 W) were placed above recirculating tanks, on a 12hr on/12hr off cycle. Salinity was kept at approximately 15 ppt; water temperature was kept in between 28-29^{o}C; ammonium levels were kept below 0.40 ppm. Redfish were fed bait live grass shrimp during captivity, while the shrimp were fed wet cat food. Experiments were run between May 25 and July 1, 2010.

Experimental mesocosms.

All trials were conducted in 2 recirculating, rectangular fiberglass tanks (length x width x height; 180 x 90 x 35 cm) located side by side, in an adjacent room from the holding tanks located in the Department of Veterinary Science building. Tank water depth was maintained at 30 cm. Water quality characteristics (salinity, temperature, dissolved oxygen) were measured before and after each trial using a YSI model 556 Multiprobe (YSI Inc., Yellow Springs, OH, U.S.A.) and ammonia concentration was measured using Hach Master Test Kit (Hach Company, Loveland, CO, U.S.A.). Fluorescent lights (40 W) were placed above the experimental tanks and a 12:12 hr light-dark regime was maintained throughout the experiment. A clear plexiglass cover was placed on top of each experimental tank to reduce potential escape by either species.

Habitat structural complexity treatments of six distinct levels was created using clean, unaggregated oyster shells (Table 1). Two aspects of complexity were tested: (1) quantity: volume of habitat created, measured by water volume displacement, which was correlated with shell number, and (2) quality: interstitial space available, measured by reef height, with equal volumes used. Each experimental reef (45 x 60 cm) covered approximately 20% of the tank bottom, with the remainder of the tank bare. Pilot runs involving both predator and prey indicated there were no so-called corner effects (Humphries 2010), thereby eliminating the need to have the corners of the tank rounded with plastic.

Treatment	Reef Volume (L)	Shell #	Vertical Relief (cm)	Prey #	Prey: Volume	Prey: Shell
Control	0	0	0	40	40:0	40:0
Low	2	40	< 5	40	20:1	1:1
Low Interstitial	2	40	10-15	40	20:1	2:3
Medium	3	75	10-15	60	20:1	4:5
Medium Interstitial	3	75	>20	60	20:1	4:5
High	5	200	>20	120	24:1	3:5

Table 1. Table of treatment and treatment descriptors. Reef volume and shell # represent the quantity of reef habitat provided. Vertical reef represents the mean height of the structure. Prey numbers were varied in several treatments to account for encounter rates with higher complexity treatments, and this is captured in the prey: volume displacement ratio. Interstitial treatments held the quantity of habitat constant while increasing interstitial space (quality) available for prey. Reef height varied with these treatments and was included in the statistical model. Created reefs covered an area of 45 x 60 cm.

Experimental trials.

All treatments were replicated 5 times (6 treatments x 5 replicates; n = 30), each assigned randomly to experimental tanks and days. Each trial was run for 24 hr and consisted of first partitioning the tank (separating the reef area) with a clear plexiglass barrier. For each trial, randomly selected shrimp were added to the side of the tank with the reef and one randomly selected red drum (starved for 48 hr) was added to the other side. Before each experimental run began, the selected predator species were starved for a 48-hour period (Heck and Thoman 1981, Canion and Heck 2009). Pilot runs in order to determine natural shrimp mortality and recovery rate were performed before any of the experimental runs started (100% recovery). A set number of grass shrimp matching the amount used in each treatment were placed in the experimental tanks and allowed a 24-hour interaction period with each of the created oyster reef structures. The oysters were pulled and prey were quantified. Other pilot runs were previously executed in order to determine necessary acclimation period, interaction period, and to determine the numbers of prey per treatment level (Humphries 2010). Initial observations indicated that red drum needed time to acclimate to their new surroundings (> 1 hr; Humphries pers. obs.); organisms were allowed 2 hr to acclimate before removing the barrier and the trial allowed interactions for 22 hr. After each trial was complete, the red drum was removed followed by the oyster shell. Remaining shrimp were then quantified and removed, and water quality (salinity, temperature, dissolved oxygen, ammonia) measured.

Treatments varied number of prey in order to try to control for encounter rates between prey and predators and to mimic densities that would be expected in the wild, as per Matilla et al. 2008 and Canion and Heck 2009. This experimental setup allowed for controlled predator and prey interactions in response to different treatments in oyster reef structural complexity (quantity, quality), while controlling for encounter rates. Predator and prey species were not used in consecutive experimental runs (Heck and Thoman 1981, Stunz and Minello 2001).

Statistical Analysis

All data were tested for normality and homogeneity; no transformations were necessary (Sharpiro-Wilk's $W=0.76$; $p<0.05$). A nested ANOVA with reef volume (height) as the two factors was run with foraging success (% eaten) as the response variable. LSMeans was used to detect significant differences, post-ANOVA (SAS Institute, Inc., Cary, NC, U.S.A.; version 9.1). Day, tank, and fish were included as randomized block factors and the model was independent of order. Data are reported as mean ± 1 SE unless indicated differently.

Results

The foraging success of red drum on grass shrimp (% shrimp consumed) differed significantly only by volume of reef (*F=97.53*, p<0.0001) (Fig. 1). Adding interstitial space did not influence foraging success. Highest foraging success was in the control treatment (88.5 ± 5%), which was significantly higher than all other treatments. Reefs with a volume of 2 L (with height 5 cm and 15 cm) were similar to one another (5 cm: 36.0 ± 3.8%; 15 cm (45.5 ±5.2 %) and had significantly higher foraging success as compared to either the medium (pile: 20.0 ± 1.1%; structure: 23.7 ± 1.9%) or high complexity reefs (13.9 ±1.9%), which did not differ significantly from one another.

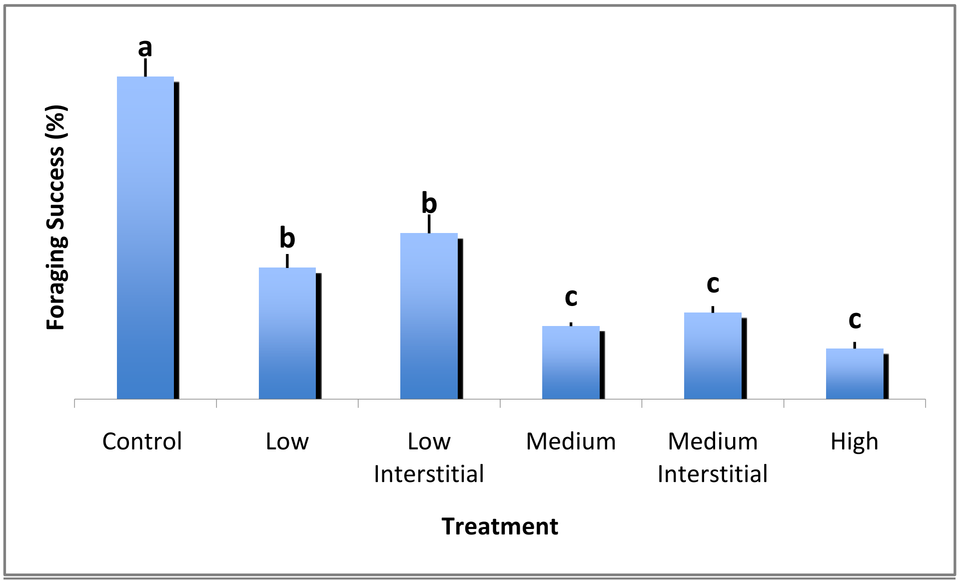

Figure 1. Foraging success (%; mean ± 1 SE) of red drum on grass shrimp. Treatments along the x-axis represent different levels of reef quantity (measured by shell volume: Control = 0 L, Low = 2 L, Medium = 3 L, High = 5 L) and interstitial space (IS = space; NS = shell pile) L- 2 L, L_, -2 L, M- 3 L, M_-3 L, H- 5 L.) and reef height/interstitial space (C-0 cm, L-< 5 cm, L_-10-15 cm, M-10-15, M_->20 cm, H- >20 cm). By structural complexity and interstitial space, denoted by oyster shell density (n=30). Treatments with different letters were significantly different (p<0.05)

Discussion

Foraging efficiency of red drum on grass shrimp was reduced by the presence of oyster reef structure; and this reduction increased as reef volume (complexity) increased. However, foraging efficiency did not differ between the two higher volume reefs suggesting a threshold at which the provision of complex structure fails to enhance the refuge value of the reef. Furthermore, the addition of large amounts of interstitial space to the oyster reef provided increased habitat complexity (i.e., quality), yet did not provide any significant differences in refuge value from the previous low and medium density reef habitats. Low and medium volume reefs of different interstitial space conformation and reef height differed only by volume of reef.

These findings are significant in that they indicate that reef volume and not reef height or increased size of interstitial space is more important in controlling foraging efficiency, and that, reef presence, per se, may be more important than reef complexity characteristics in affecting foraging.

Patterns of encounter rates may differ for different predator-prey combinations and the specific habitat being tested (Rilov et al. 2007). Furthermore, the specific habitat characteristics that might influence predator-prey dynamics may vary with different species combinations. One important aspect though is ratio dependence - where impacts are dependent on the ratio of the prey population size to the predator population size, and not the absolute numbers of either species (Abrams and Ginzburg 2000). In this study, we attempted to match predator and prey densities with the complexity of the reef to mimic natural environments, and to maintain natural encounter rates. This is in contrast to many published papers (Nelson 1979, Heck and Thoman 1981) which have run controlled laboratory experiments trying to show how structural complexity affects predator foraging success by using constant predator:prey ratios in order to avoid confounding the effects of variable encounter rates and structural complexity. Recently, this approach was questioned for seagrass systems (Matilla et al. 2008, Canion and Heck 2009) and, in contrast to most previous work, results varying predator and prey ratios to maintain constant encounter rates suggested that only structure per se determines foraging success. Our study varied prey density with habitat complexity (quantity) and found that there was a step response with one threshold. This model falls in between that of Nelson (1979) who demonstrated a multiple step model using a constant predator and prey number, and that of Matilla et al. 2008 who found that increasing structural complexity (in seagrass) failed to increase prey survival when prey and predator densities were increased.

Defining habitat complexity still remains a matter of debate among scientists, and may differ across habitats. For oyster reefs, the interstitial space provided is often cited as a reason for its provision of valuable prey refuge habitat (Grabowski and Powers 2008). Interstitial space is an empty space or gap between spaces full of structure or matter. This space in-between the structure can help provide refuge for the hiding prey as long as the size of the gap in the structure is large enough for the prey to fit in, but small enough that the predator cannot reach in (Warfe et al 2008). Thus, for oyster reefs, interstitial space, volume, density, and structure height can all play a valuable factor is defining complex habitats. Our results showed that reef volume, not reef height or reef interstitial space, made significant differences in our predator's foraging efficiency. Also there appeared to be a threshold where this foraging efficiency was significantly different. The results of this study agree with the same basic concepts put forth by other studies in the recent years (Nelson 1979, Heck and Thoman 1981, Adams et al 2004) but differed from that of Heck and Canion (2009) and Matilla et al (2008) who failed to find an impact of increasing complexity on foraging efficiency. Interestingly, using the oyster reefs and the same predator and prey, but holding prey numbers constant across complexity treatments, our study results were identical to those of Humphries (2010), even though we increased prey numbers.

The results of this experiment show that habitat complexity, specifically oyster reef volume, is a major factor affecting a predator's foraging efficiency. Specifically, only volume of the created reef, and not the provision of extra height or interstitial space were important in influencing foraging success rate. More importantly, this study was able to show that even when prey densities increased with quantity of structural habitat, this finding held true indicating that there were no density dependent processes at work with decreasing encounter rates. The lack of an effect of interstitial space may be due the fact that the piles of shell (limited interstitial space treatments) still provided important hiding spaces for the prey and/or that the created interstitial space treatments provided spaces that were too big to provide good refuge. Thus, while the interstitial low and medium treatments provided more mobility to access to the inside of the reef; it still provided the same amount of hiding spaces, albeit wider open spaces than just the pile of shell. Soniat et al (2004) showed that shell orientation might play an important role in determining the refugia available for resident species on an oyster reef, noting that resident species have a high affinity towards vertically oriented shell. Although the shell in our experiment was horizontally oriented, clearly, there are many qualitative variables related to complexity that still remain that are difficult to quantify.

Habitat complexity does affect predator-prey relationships by interfering with the predator's ability to easily capture and devour its prey. The increased structure provided by the reef potentially creates valuable refuge for the prey species. This study shows that at some point, increased habitat complexity reaches a threshold level where extra structure does not affect the trophic relationship between predator and prey. Determining at what point, structural complexity may be redundant, or, whether other qualitative aspects of structural complexity account for the value of complexity remains to be done.

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